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## GALTONIAN REGRESSION IN THE "PURE LINE" *

By George Harrison Shull

Among the experiments undertaken this year at the Station for Experimental Evolution for the purpose of investigating the inheritance of characters in plants, was one intended to be essentially a repetition of Johannsen's studies † in the inheritance of seed-weights in beans. The variety of *Phaseolus vulgaris* chosen for this study proved to be unsatisfactory from a technical standpoint and it is not proposed to pursue the experiment further with this material, though several subsidiary questions may be taken up in other plants. The relation between the results of Johannsen on beans and those of Galton on sweet-peas ‡ have appeared on further analysis to be in need of reinterpretation rather than reinvestigation, and the writer feels justified, therefore, in taking this abandoned experiment as a text for such reinterpretation.

From a number of statistical studies upon various characters in man and animals and a single series of experiments in sweet-peas, Galton derived his law of natural inheritance and its corollary — the law of regression from mediocrity. || The law of natural inheritance is, briefly, that the offspring of any

* Presented before Section G, A. A. A. S., at Philadelphia, December 30, 1904, under title of "Inheritance in Pure Lines."

† Ueber Erblichkeit in Populationen und in reinen Linien. Jena: Fischer, 1903.

‡ Natural inheritance. New York: Macmillan & Co., 1889.

|| This has frequently been called "regression *toward* mediocrity," but as the coefficient of regression is measured *from* the mean condition of the population confusion has arisen through expressing it in this way. Galton's own inconsistency in discussions of regression is doubtless responsible for this confusion. He first presents it clearly as a deviation *from* mediocrity, but later says there is "no regression at all" when this deviation is equal in the two kinships under comparison, and the coefficient of regression is unity. *Cf.* Natural inheritance 95–98 with 132–133.)

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parentage, when considered in its entirety, inherits one-half its characteristics from its parents, one-fourth from its grandparents, one-eighth from its great-grandparents and so on. The law of regression from mediocrity points out that the children of extreme parents are not on the average so extreme as their parents, though they deviate in the same direction from the mediocre condition of the race. As an example of regression, take Galton's results on sweet-peas: The diameter of parent seeds which produced plants having on the average seeds of the same diameter was 3.94 mm. Assuming this to be the mediocre condition of the strain he was using he found that whatever the parental deviation from this diameter the mean filial deviation was in the same direction, but only one-third as great. Thus the offspring from seeds 5.34 mm. in diameter produced seeds having an average diameter of $3.94 + \frac{5.34 - 3.94}{3} = 4.41$ mm. (observed diameter, 4.44 mm.).

Johannsen obtained similar results in beans when he compared the average weight of seeds in the offspring with the weight of the parent seeds, if the latter were selected solely with reference to the weight of the individual seeds and without regard to the pre-parental ancestry; but when he separated the individual "pure lines" he found that the mean weight of seeds in the offspring is the same on the average as that of the preceding generations in the same "line," in other words, plants produced from small seeds bear seeds of the same average weight as do plants which are produced from large seeds having the same ancestry.

By the "pure line" Johannsen means a series of individuals related only through the process of self-fertilization. On *a priori* grounds it seems proper to apply the term to every series of individuals that do not combine the elements of two or more ancestral lines through the equivalent of a sexual process. Thus, so far as hereditary qualities are concerned, there should be no reason to expect in a self-fertilizing population, conditions different from those in a population related through budding or other method of vegetative reproduction, provided of course, that the self-fertilizing population has not been so recently modified by a cross as to allow the analysis and recombination of characters derived from different ancestral lines.

The complete return of the offspring of an extreme parent, to the mean condition of the "pure line" to which it belongs, or in technical language the entire want of "regression" in the "pure line," is presented by Johannsen as a fundamental exception to the conclusions of Galton.

Weldon and Pearson have criticized * the work of Johannsen in considerable detail and although the tone of their criticism is adverse throughout, they grant that his main contention may well be true, that small seeds and large seeds of the same plant do not give rise to plants bearing small seeds and large seeds respectively. If read aright, their criticism must be held to be confirmatory in so far as Johannsen's data are capable of biometric analysis. Certainly their conclusion that his results are closely identical with those found for other plants and for animals when we compare *mean* parental and *mean* filial characters, agrees precisely with that reached by Johannsen, for these *means* represent the condition in the *population* or mixture of several "pure lines," and not in the individual "*pure line*."

The relation between this work of Johannsen and that of Galton on sweet-peas may now be considered. In the first place, the actual results were the same when the treatment of the material was the same, and in so far the work of Galton was confirmed; but when the "pure lines" were followed separately they were found to offer an apparent exception in the complete return of the offspring of extreme parents to the mean condition of the "pure line." Instead of this being fundamentally opposed to Galton's results, however, it is the condition which should have been derived *a priori* from Galton's "Law of natural inheritance."

Regression is lucidly explained by Galton † as due to the fact that the child inherits partly from his parents, partly from his more remote ancestry, and that if "traced far backwards his ancestry will be found to consist of such varied elements that they are indistinguishable from a sample taken at haphazard from the

* Inheritance in *Phaseolus vulgaris*. Biometrika, 2: 499-503. N 1903.

† Natural inheritance, 105.

general population, . . . in other words it will be mediocre." Now, if the mean condition of the parental generation and of each preceding generation in the same line deviates to the same degree from the mean condition of the population, it becomes an inevitable inference that in so far as hereditary influences are concerned, the offspring must have the same mean character regardless of the largeness or smallness of the individual seeds from which those offspring have developed.

This "fixity of type" which Johannsen finds in the "pure line" was recognized by Galton in his treatment of pure breeds* and it seems strange that he did not perceive that his sweet-peas which he recognized and described as a self-fertilizing population were at variance with this fixity of type in the pure breed. Johannsen has brought harmony in Galton's results where there was a previously unnoted discord, and has confirmed the laws of "natural inheritance" and of "regression from mediocrity" as applied to the characters of self-fertilizing populations.

An important point which is brought out by these results of Johannsen both from a scientific and an economic standpoint is that the weight or size of an individual seed is not the hereditary unit, but the character of all the seeds of each plant considered as a whole. A plant which produces small seeds in general, may produce some seeds which are larger than the smallest seeds of another plant which produces large seeds in general, so that when the student of heredity wishes to use seed-characters or presumably any other repeated character, he must seek the general condition of the character in question in each plant and not depend upon the character of single seeds or single other repeated organs.

The economic application of this important principle is obvious. It has been very generally maintained by horticulturists that varieties deteriorate as the result of the selection of small seeds, tubers, etc., for propagation, but this proposition, while satisfying a certain sense of logic, has rested on no scientific research. The fixity of type in the "pure line" which now appears to be established, shows that no such deteriorating effect

* Natural inheritance, 189.

will be produced so long as the seeds are large enough to produce vigorous plants.

The farmer and the plant-breeder may plant the small potato tubers or the small seeds without any danger of deterioration in the yield and quality of the crop provided they select these tubers or seeds from plants which yield the largest quantity and the finest quality of tubers or of seeds.

STATION FOR EXPERIMENTAL EVOLUTION,
COLD SPRING HARBOR, LONG ISLAND.

## SOIL WATER IN RELATION TO TRANSPIRATION

BY V. M. SPALDING

In a recent article by the writer on the creosote bush in its relation to water supply,* the statement was made that the amount transpired appears to stand in direct relation to the amount of water available in the soil in which the plant is growing. Further observations on this and some other desert plants not only confirm this view but go to show that water in the soil is a controlling factor, and that even as efficient an agent as light may, in comparison, take quite secondary rank.

The later literature of transpiration, however voluminous in general, is extremely limited as regards this branch of the subject.† Aloi and Ferruzza have shown that the amount of water in the soil is a factor by which the opening of stomata, and consequently the rate of transpiration, is controlled, and Stenström has attempted to formulate a mathematical equivalency between the rate of transpiration and the ratio of atmospheric and soil moisture. The remaining literature dates from the works of Sachs and older writers.

In the summer of 1904, while engaged in observing the influence of light of different degrees of intensity on transpiration, I found that results apparently conflicting became consistent when account was taken of the amount of water supplied to the plants under investigation and the time at which it was given.

* Botanical Gazette, 38: 122. 1904.

† Burgerstein, A. Die Transpiration der Pflanzen, 137. 1904.